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DNA and spores from coprolites reveal that colourful truffle-like fungi endemic to New Zealand were consumed by extinct moa (Dinornithiformes)

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Mycovores (animals that consume fungi) are important for fungal spore dispersal, including ectomycorrhizal (ECM) fungi symbiotic with forest-forming trees. As such, fungi and their symbionts may be impacted by mycovore extinction. New Zealand (NZ) has a diversity of unusual, colourful, endemic sequestrate (truffle-like) fungi, most of which are ECM. As NZ lacks native land mammals (except bats), and sequestrate fungi are typically drab and mammal-dispersed, NZ's sequestrate fungi are hypothesized to be adapted for bird dispersal. However, there is little direct evidence for this hypothesis, as 41% of NZ's native land bird species became extinct since initial human settlement in the thirteenth century. Here, we report ancient DNA and spores from the inside of two coprolites of NZ's extinct, endemic upland moa (*Megalapteryx didinus*) that reveal consumption and likely dispersal of ECM fungi, including at least one colourful sequestrate species. Contemporary data from NZ show that birds rarely consume fungi and that the introduced mammals preferentially consume exotic fungi. NZ's endemic sequestrate fungi could therefore be dispersal limited compared with fungi that co-evolved with mammalian dispersers. NZ's fungal communities may thus be undergoing a gradual species turnover following avian mycovore extinction and the establishment of mammalian mycovores, potentially affecting forest resilience and facilitating invasion by exotic tree taxa.

1. Introduction

Ecological networks often comprise thousands of interconnected species, meaning species losses can produce cascades that impact entire ecosystems [1]. Faunal declines and extinctions have characterized the late Quaternary (*ca* 50 ka to present), with megafauna and island endemics being among the worst affected [2–5]. The extent of recent broken species interactions may be reflected by the prevalence of taxa hypothetically adapted for absent partners (evolutionary anachronisms) [6,7]. For example, numerous plant species worldwide produce fruit that cannot be dispersed by indigenous extant species (e.g. owing to overlarge seeds or unpalatability) and were presumably dispersed by extinct fauna such as megafaunal mammals (e.g. proboscideans or ground sloths) [6–12] or giant tortoises [13–17]. Although some anachronistic plant taxa have benefitted from introduced surrogates [18–22], or have

been domesticated [23–25], others are range-restricted, recruitment/dispersal limited, or in severe decline [8,16,26–28], suggesting that the long-term effects of faunal loss are still unfolding in many ecosystems as 'extinction debt' [29–31].

Although disrupted animal–plant mutualisms are frequently presented as a likely consequence of faunal extinctions [32–37], how fungi have been affected by the loss of animal mutualists is poorly understood [38,39]. Animals that consume macrofungi sporocarps (mycovores) can disperse viable spores via their scats, resulting in an animal–fungi propagule dispersal mutualism [40–46]. Most spores shed by agaricoid (mushroom-forming) species tend to congregate near sporocarps, and those that successfully wind-disperse are highly diffuse in where they settle [47,48]. In contrast, animal-consumed spores are deposited in a rich growing medium at high concentrations and often far from the parent [43,49]. Furthermore, sequestrate (truffle-like) fungi do not forcibly discharge their spores, and mostly depend on mycovores for spore dispersal [50]. Sequestrate morphology has evolved independently across many macrofungal phyla and repeatedly within some genera (e.g. *Cortinarius* or *Russula*) [51–54], supporting that mycovores provide a reliable alternative for spore dispersal over wind transport. As many animal-dispersed fungi are ectomycorrhizal (ECM) with ecologically important plants (e.g. canopy-forming trees) [55], animal dispersal of ECM fungi can result in a tripartite animal–plant–fungal mutualism underpinning functions such as forest stability, productivity, regeneration and expansion [39,44,46,49,56–60]. Sequestrate fungal sporocarps are typically drab and often hypogeous (below-ground) and/or odorous [61–65], evidently reflecting adaptations for scent-foraging and digging species with poor colour vision (e.g. most mammals), rather than diurnal, visual-foraging species with low olfaction capability (e.g. most birds) [66]. Congruently, most known examples of vertebrate mycovores are mammals [67], with fewer documented examples of reptile [68] or bird [69,70] mycophagy.

Many sequestrate fungi endemic to New Zealand (NZ) produce brightly coloured, epigeous (above-ground), fruit-like sporocarps, which may be adaptations for bird dispersal [71–73]. However, it has been difficult to test the hypothesis that NZ's fungi were bird-dispersed as most of NZ's native bird species are either extinct or severely range-reduced. NZ's long oceanic isolation from Gondwana (over 52 Ma) [74] produced a complex, mammal-free terrestrial biota (excluding bats or pre-Quaternary taxa) dominated by birds, including nine species of megaherbivore ratite moa (Dinornithiformes) spanning approximately 14–242 kg in weight [75,76]. The arrival of humans and introduced mammals to NZ after AD thirteenth century [77] resulted in the extinction of *ca* 41% of NZ's native terrestrial bird species [78] and all moa by the sixteenth century [79,80]. Further, many of NZ's surviving bird species are functionally extinct [81,82]. Avian mycophagy has rarely been observed in NZ, leading to speculations that NZ's colourful sequestrate fungi are evolutionarily anachronistic and that the primary avian mycovores in NZ consisted of extirpated or extinct taxa such as moa [71,72,83]. NZ's forests are heavily composed of widespread tree species co-dependent on ECM fungi, including southern beech (Nothofagaceae), mānuka (*Leptospermum scoparium*) and kānuka (*Kunzea ericoides*) [84]. As most of NZ's sequestrate fungi are believed to be ECM [85], evidence for their dispersal by extinct birds would indicate that the full ecological consequences of these extinctions are yet to be realized in NZ forests [86].

Hundreds of Holocene avian coprolites, identified by ancient DNA (aDNA) as mostly being deposited by five species of moa and the endangered kākāpō parrot (*Strigops habroptila*), occur at several localities on NZ's South Island [87]. Although a previous study on 18S rRNA metabarcoding of kākāpō, upland moa (*Megalapteryx didinus*), and South Island giant moa (*Dinornis robustus*) coprolites identified the presence of ECM fungi [86], taxonomic resolution was insufficient to confirm whether the fungi were sequestrate. Further, although moa coprolites have been previously analysed for palynomorphs [88–90] and parasites [91], they have not been investigated for fungal spore content and concentrations (spores mg^{-1}). As a result, there is limited evidence that moa consumed sporocarps or truffle-like fungi specifically or played a role in the dispersal of their spores. Although there is circumstantial evidence that NZ's sequestrate fungi are adapted for bird dispersal and were likely consumed by extinct birds such as moa [92], higher taxonomic resolution and spore evidence are needed to definitively answer the question: 'did moa consume, and potentially disperse, NZ's truffle-like fungi?'

2. Methods

Here, we report an opportunistic discovery from two coprolites that were originally sampled as part of a larger project on kākāpō coprolites and unexpectedly determined by aDNA as being from the relatively small (compared to other moa, approx. 14–63 kg) [76] upland moa [93]. The coprolites (figure 1) were from Hodges Creek (HC) Cave near the upper Tākaka River catchment in northwest Nelson (sample X/17/11/33, site elevation approx. 900 m), and Takahē Valley (TV) in Fiordland (sample X18/153/03, site elevation approx. 1100 m). HC Cave is surrounded by dense silver beech (*Lophozonia menziesii*) forest, and the coprolite (collected in 2018 by authors of this study) was located approximately 20 m into the cave system, partially covered in sediment and large rock fragments [93]. The TV sample, conversely, was from a museum specimen (CM 2016.171.11) with a less certain collection date and provenance. However, coprolite deposits in TV have been found in several rockshelters, and are all located adjacent to subalpine vegetation near to a silver beech-dominated treeline [93].

Specialist coprolite-subsampling procedures, ^{14}C dating, DNA extraction, DNA amplification and species identification of both samples are described in [93]. To minimize the risk of exogenous environmental contamination, the exterior of the coprolites was scraped off with a sterile scalpel, and the coprolite was then ultraviolet-radiated for 15 min before a subsample was taken from the interior of the coprolite under a sterile hood in a clean room designed for palaeoecological samples. All DNA extraction and PCR preparation were performed in a purpose-built, isolated aDNA laboratory. In addition to the two coprolite DNA extractions, we included extraction blank controls (EBCs, extractions performed without the addition of sample, to identify contaminants) from [93].

DNA extractions (both samples and EBCs) were amplified in triplicate for a region of the noncoding, nuclear gene Internal Transcribed Spacer 1 (ITS-1) using the fungi-specific primers ITS5 [94] and ITS5.8S [95] (initial 2 min denaturation of 94°C; 35

Figure 1. (*a*) Upland moa skeleton, (*b*) HC coprolite X17/11/33, and (*c–h*) examples of fungi identified from aDNA (* denotes taxa with congruent spore evidence): (*c*) *Gallacea scleroderma**, (*d*) *Gallacea* sp. 'Nelson Lakes'*, (*e*) *Rossbeevera pachydermis**, (*f*) *Russula macrocystidiata**, (*g*) *Cortinarius* sp. 'Blyth Track', (*h*) *Cortinarius violaceovolvatus*. Photo credits: (*a*) Wikimedia Commons, (*b*) Alexander P. Boast, (*c–h*) Noah Siegel.

cycles of 30 s at 94°C, 30 s at 60°C and 40 s at 72°C; and a final extension of 10 min at 72°C). We selected ITS5 and ITS5.8 as these primers have been shown to reliably amplify a broad diversity of fungi (including Ascomycota and Basidiomycota) from ancient samples [95]. Reagents, PCR preparation, indexing, quantification, library preparation and sequencing of amplicons, as well as early bioinformatic processing (e.g. demultiplexing, primer removal and quality filtering) followed [93]. Identifications used a reference database built from all ITS fungal sequences on GenBank (https://www.ncbi.nlm.nih.gov/genbank/) identified to family level. FASTA files representing all amplicon sequence variants (ASVs) were analysed using the BLASTn algorithm in BLAST+ v. 2.7.1 [96], against our database, using parameters described in [93]. BLASTn outputs were processed using MEGAN v. 6 [97], using parameters optimized to detect taxa rather than provide conservative identifications: the top 5% of hits, a minimum percentage identity of 80%, and a bitscore cut-off of 200. All ASVs identified in an EBC control were removed from subsequent analyses. Further, all ASVs attributed to macrofungi or ECM fungi (none of which appeared in EBC controls) had their taxonomic identity confirmed by maximum-clade credibility Bayesian phylogenetic analyses in MrBayes, using a series of selected outgroup taxa and a substitution model identified by jModeltest v. 2.1.10 [98], 1×10^7 generations and discarding 25% of trees as a burn-in (electronic supplementary material, figures S1–S6).

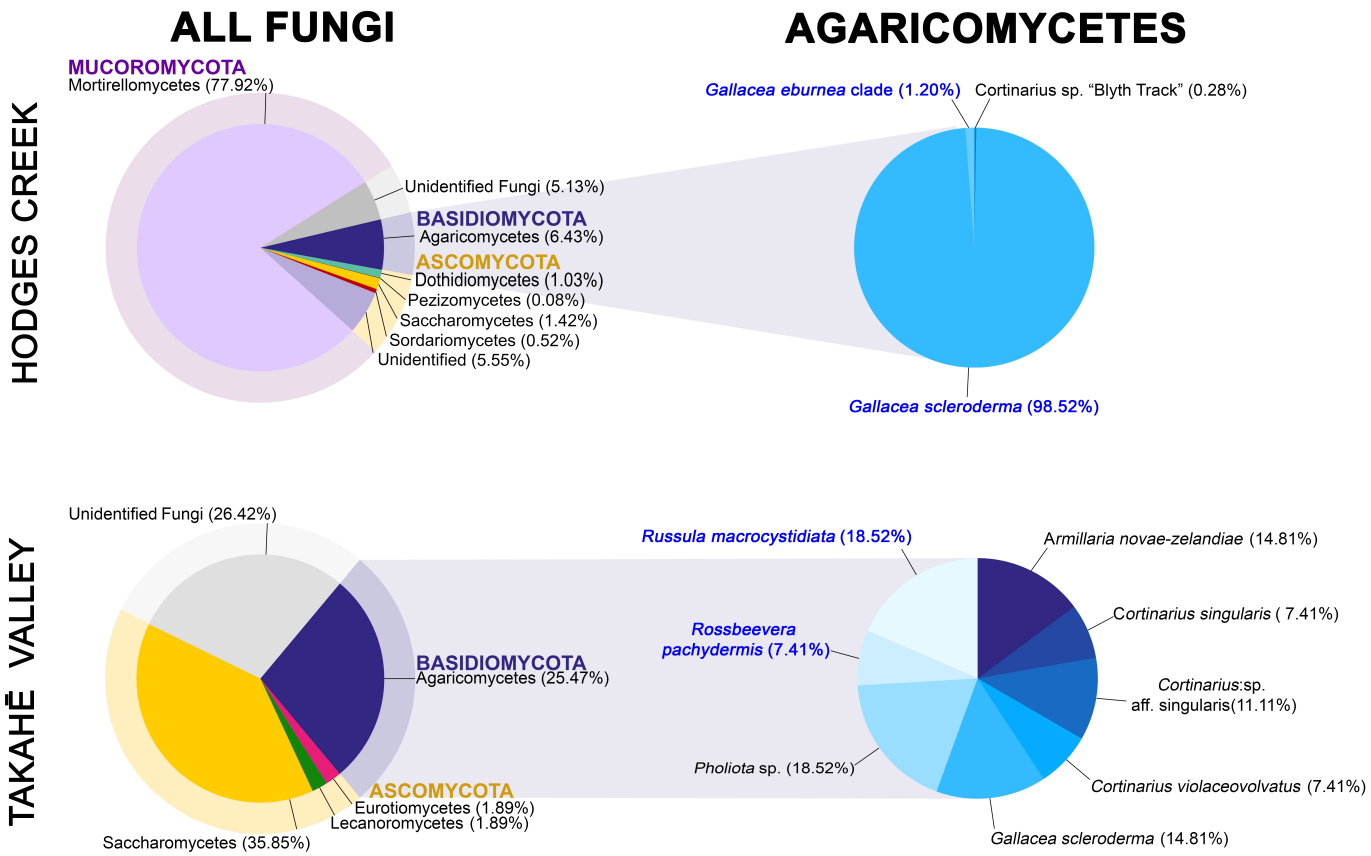

Figure 2. Percentage of reads assigned to taxa from the two coprolite samples, subdivided into all fungi (left) and Agaricomycetes only (right). Taxa coloured blue are those with congruent spore evidence in the coprolites, and most likely to be dietary.

Spore identification was performed on microfossil slides prepared using methods in [93], omitting the acetolysis and staining steps. During microfossil preparation, a known number of exotic *Lycopodium clavatum* marker spores were added (University of Lund, batch no. 1031, 20 848 spores per tablet, on average). Fungal spores were identified at 1000× magnification (oil immersion) and were compared with those available for collections deposited in the Plant Disease Division Fungarium, using online imagery available via the Systematic Collection Data website (https://scd.landcareresearch.co.nz/) and the Biota of New Zealand website (https://biotanz.landcareresearch.co.nz/). Fungal spores and *L. clavatum* spores were subsequently counted at 200× magnification until at least 250 fungal spores were counted. Known weights of the microfossil subsamples, compared with *L. clavatum* counts, meant that the mass of counted samples and fungal spore concentration could be estimated.

3. Results

Fungal DNA assemblages from both HC and TV [99] were dominated by saprobic, microfungal Mucoromycota and Ascomycota (figure 2; electronic supplementary material, dataset 1), which could not be confidently distinguished from common environmental species, were unlikely to be dietary, and were not analysed further. All remaining fungal diversity comprised macrofungal Basidiomycota in the Agaricomycetes (6.4 and 25.5% of reads from the HC and TV samples, respectively; figure 2). Unlike microfungal Ascomycota or Mucoromycota, macrofungal Agaricomycetes had the potential to be dietary. For example, all genera of Agaricomycetes we detect produce sporocarps large enough to be foraged on by mycovores (electronic supplementary material, dataset 1). Further, most identified Agaricomycetes sequences were of habitat-specific ECM taxa, which are unlikely to be laboratory contaminants (e.g. no ECM fungi were detected in EBC controls) or to colonize coprolites *in situ* (neither coprolite was associated with forest soil, and ECM fungi depend on symbiotic tree roots for development) [86]. Hereafter, percentage statistics are derived from Agaricomycetes only.

Thirteen ASVs were identified as native macrofungal Agaricomycetes. Most were identifiable to species, either by close pairwise match (nine showed more than 98.5% similarity to reference sequences) (electronic supplementary material, dataset 1) and/or by phylogenetic association (electronic supplementary material, figures S1–S6). Of these, ECM sequestrated fungi were dominant (figure 1), especially the purple *Gallacea scleroderma* (95.5% of HC and 14.8% of TV), the purple *Cortinarius violaceovolvatus* (7.4% of TV) and the drab (but staining blue with bruising or exposure to air) *Rossebeevera pachydermis* (7.4% of TV). Low proportions of HC reads were also identified as falling within, or related to, a clade of two near-identical, drab/pale pink *Gallacea* species (*G. eburnea*, *G.* sp. 'Nelson Lakes'). Agaricoid species included the ECM *Russula macrocystidiata*, and *Cortinarius* spp., the saprobic *Armillaria novae-zelandiae* and an unidentified *Pholiota* (a saprobic genus). High concentrations of spores with morphologies congruent with those of the ECM fungi genera *Gallacea* were identified from HC (1885 spores mg^{-1}, occasionally in clusters admixed with fungal tissue) and *Rossbeevera* and *Russula* from TV (7205 and 3556 spores mg^{-1}, respectively) (electronic supplementary material, figures S7 and S8). These spore concentrations fall within the range observed in the dung (by dry weight) of contemporary avian mycovores, and strongly support sporocarp consumption [70].

4. Discussion

Here, for the first time, we present co-occurring fungal spore and species-level fungal DNA evidence from moa coprolites. Together, these two sources of data provide definitive support that upland moa consumed the sporocarps of ECM fungi, including brightly coloured sequestrate species (figures 1 and 2). ECM fungi are extremely unlikely to colonize coprolites *in situ*, as ECM fungi depend on symbiotic tree roots for development and would therefore have been unable to colonize moa coprolites located in dry, root-free sediment away from forest soil. Furthermore, those fungal species with supporting DNA and spore evidence were low in richness (one sp. HC, two spp. TV) and were represented by high spore concentrations. In comparison, environmental spore contamination or incidental spore consumption by moa would likely result in a wider variety of spore types and much lower spore concentrations. Further, consumption of other fungal tissues is not supported (e.g. moa incidentally consuming hyphae and forest soil when feeding on the forest floor), as such tissues are not associated with spores. Conversely, our spore data would have been of limited value without DNA evidence, as fungal spores are extremely difficult to identify to species through morphology alone. Our study thus builds considerably on the study of Boast *et al*. [86], who identified ECM-specific fungal genera from moa coprolites (*Cortinarius*, *Inocybe*) but lacked spore evidence and were unable to provide species-level resolution or detect sequestrate species. Overall, this new discovery confirms an interaction between two geographically separated moa (almost 600 km) and coloured sequestrate fungi (and ECM fungi in general). As consumption is also likely to have resulted in spore dispersal, we thus infer that this interaction represents a lost mutualism.

At least three species of ECM fungi had co-occurring spore and DNA observations in our data: at least one species of the sequestrate genus *Gallacea* (strongly supported by DNA read percentages to be the purple *G. scleroderma*), the drab to blue sequestrate species *R. pachydermis* and the agaricoid species *R. macrocystidiata* (figure 1). Although other fungi detected in the DNA data were not observed in the spore counts (e.g. the 'purple pouch fungus' *C. violaceovolvatus*), these could represent consumed sporocarps in some cases. For example, if sporocarps were consumed prior to sporulation, spores would either be absent or potentially too undeveloped to survive digestion, preservation or laboratory procedures [100]. All moa species with gizzard or coprolite records consumed brightly coloured fleshy fruit, suggesting that they were visual foragers and would have been attracted to similarly coloured fungi [101]. Other ratites, such as emu (*Dromaius novaehollandiae*) [102] and southern cassowary (*Casuarius casuarius*) [103] consume agaricoid fungi, and upland moa, giant moa (*Dinornis* spp.) and little bush moa (*Anomalopteryx didiformis*) foraged on forest floors [86,88,90,101,104]. While our data demonstrate that at least one moa species consumed sequestrate fungi, it is likely that most other moa species did too, given their generalist diets and high degree of dietary overlap between species [86,88,101]. Further analyses of moa coprolites will be required to reveal whether sequestrate fungi consumption was a common and widespread activity among moa.

Although NZ's presettlement avifauna was diverse, moa may have been exceptional fungal dispersers. The fibrous diets of herbivorous moa, osteological evidence and allometric scaling imply that moa had larger digestive systems and home ranges and longer gut retention times than other NZ ground-dwelling birds [101,105–107]. An extant large ratite, the common ostrich (*Struthio camelus*), has an average retention time for small particulates of 30–36 h [108]. Moa could thus have dispersed spores from any consumed fungus across substantial distances and during several deposition events. Some moa species had broad ranges, with upland moa evidently moving between lowlands, forests and alpine herbfields [75,90,109], meaning they could have contributed to the fungal spore inoculation of soils in non-forest habitats and thereby assisted with forest spread and regeneration [57,60]. Of NZ's surviving avifauna, only the critically endangered kākāpō, North Island robin (*Petroica longipes*) and weka (*Gallirallus australis*) have been observed to consume fungi [69,73]. However, robins and other small birds (e.g. passerines, including introduced species) may be limited dispersers, as they have short gut retention times and typically have small home ranges [110–112]. Most larger herbivorous or omnivorous ground-dwelling birds in NZ are extinct [75] or endangered [82], with only the omnivorous rail weka locally common in some regions of NZ [113]. Few introduced ground-dwelling birds occur deep within native forests [114]. Overall, moa have no functional analogues as fungal dispersers among NZ's contemporary avifauna, and the overall contribution of birds to fungal dispersal in NZ must now be heavily diminished relative to presettlement NZ.

Coloured and non-scented sequestrate fungi appear to be poorly adapted for mammal dispersal relative to bird dispersal. Brightly coloured sequestrate fungi also occur in New Caledonia (e.g. *Leratiomyces similis*, *L. smagdarinus*) [115] and Lord Howe Island (*Secotium fragariosum*) [116] which, like NZ, lack indigenous mammals (except bats) and had vertebrate faunas dominated by birds and/or reptiles [92,117,118]. Further, compared with NZ, a very low proportion of sequestrate fungi on continental ecosystems are brightly coloured (e.g. *Cortinarius atratus* in southern Australia, *Halligenea purpurea* in Patagonia) [70,119]. In NZ, introduced red deer (*Cervus elaphus*) and Australian brushtail possum (*Trichosurus vulpecula*) were observed consuming both native and exotic fungi, although only exotic fungal spores were viable post-digestion [120]. Further, in that same study [120], mammals preferentially foraged on sequestrate species that were exotic (*Rhizopogon*) or shared with Australia (*Octaviania*) [121]. As introduced mammals have largely replaced NZ's avian-dominated ground vertebrates, it can be assumed that sporocarps attractive to mammals now have an adaptive advantage over many native fungi species, being more likely to be foraged on and/or successfully dispersed.

A guild of mycovores in forested ecosystems results in a more diverse and admixed fungal community, benefitting forest productivity, regeneration and resilience [39]. Animals can inoculate unforested areas with ECM fungal spores, which may assist with forest spread or regeneration [57]. For example, the absence of symbiotic ECM in soil can limit the establishment of NZ beech [122,123]. The removal of native fungi dispersers, such as moa, from NZ's ecosystems has therefore likely resulted in a reduced dispersal capacity for many NZ fungi, possibly reducing rates of spread and regeneration of some forest types as a result. Some of NZ's ECM fungi may now be developing increasingly clustered distributions at the local scale, characteristic of dispersal-limited taxa [39], with flow-on effects for forest resilience. Further, a suite of species attractive to mammalian

dispersers may now dominate mycovore faecal ECM inoculum in NZ (e.g. in unforested areas), conceivably causing NZ's ECM communities to become increasingly biased towards non-endemic taxa [120]. This may further impact forest ecology by opening invasion pathways for trees better adapted for symbioses with exotic fungi (e.g. lodgepole pine, *Pinus contorta*) [120,124–126].

We provide robust evidence, using coprolites, that native NZ fungi were consumed by the extinct moa. Further, we strongly support the hypothesis that many of NZ's ECM native fungi were adapted for, or at least benefitted from, avian dispersal, an interaction likely to have been drastically reduced by NZ bird extinction and range contraction. Our small sample size (two coprolites) provides a key starting point for identifying this novel interaction. However, further analysis of more coprolites and modern scats from a range of different species will help to address the question of how bird–fungi interactions in NZ forests have changed over time. In conclusion, we argue that NZ's sequestrate fungi present a strong case for evolutionary anachronism, and the long-term consequences of the lost native mycovores, such as moa, may yet be fully realized in NZ's forests.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. Supporting data for this study—including raw and processed metabarcoding DNA data, alignments for phylogenetic analyses and custom-built reference database—are available on the Manaaki Whenua–Landcare Research Datastore [99].

Supplementary material is available online [127].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. A.P.B.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, software, visualization, writing—original draft, writing—review and editing; J.R.W.: conceptualization, methodology, project administration, resources, software, supervision, validation, visualization, writing—review and editing; J.C.: investigation, resources, validation, writing—review and editing; N.B.: investigation, methodology, project administration, resources, software, supervision, writing—review and editing; G.L.W.P.: conceptualization, funding acquisition, methodology, project administration, supervision, writing—review and editing; J.M.W.: conceptualization, funding acquisition, methodology, project administration, resources, software, supervision, visualization, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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